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Research paper

Can place-specific cochlear dispersion be represented by auditory steady-state responses?

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ABSTRACT

The present study investigated to what extent properties of local cochlear dispersion can be objectively assessed through auditory steady-state responses (ASSR). The hypothesis was that stimuli compensating for the phase response at a particular cochlear location generate a maximally modulated basilar membrane (BM) response at that BM position, due to the large "within-channel" synchrony of activity. This would lead, in turn, to a larger ASSR amplitude than other stimuli of corresponding intensity and bandwidth. Two stimulus types were chosen: 1] Harmonic tone complexes consisting of equal-amplitude tones with a starting phase following an algorithm developed by Schroeder [IEEE Trans. Inf. Theory 16, 85–89 (1970)] that have earlier been considered in behavioral studies to estimate human auditory filter phase responses; and 2] simulations of auditory-filter impulse responses (IR). In both cases, also the temporally reversed versions of the stimuli were considered. The ASSRs obtained with the Schroeder tone complexes were found to be dominated by "across-channel" synchrony and, thus, do not reflect local place-specific information. In the case of the more frequency-specific stimuli, no significant differences were found between the responses to the IR and its temporally reversed counterpart. Thus, whereas ASSRs to narrowband stimuli have been used as an objective indicator of frequency-specific hearing sensitivity, the method does not seem to be sensitive enough to reflect local cochlear dispersion.

1. Introduction

The frequency-place transformation that characterizes the mammalian auditory system is established in the inner ear, the cochlea, and is mainly a consequence of the mechanical properties of the basilar membrane (BM) as part of the cochlea, with an impedance that varies as a function of position (place) along the BM. The corresponding frequency analysis in the cochlea, associated with this frequency-place transformation, has traditionally been described effectively as a bank of overlapping band-pass filters (e.g. Fletcher, 1940).

The properties of these filters in humans have been estimated mainly using psychoacoustic paradigms. Based on data from behavioral masking experiments, various studies have estimated the amplitude characteristics of the band-pass filters, commonly referred to as "auditory filters" (e.g., Fletcher, 1940; Zwicker et al., 1957; Patterson, 1976; Glasberg and Moore, 1990; Rosen and Baker, 1994). More recently, there has been increasing focus on describing the auditory filters' phase response (e.g., Lentz and Leek, 2001; Oxenham and Dau, 2001; Shen and Lentz, 2009; Wojtczak and Oxenham, 2009). Such estimates of the auditory filter phase response have typically been obtained from masking experiments using tones presented in a particular type of harmonic tone complex maskers, known as Schroeder tone complexes.

Schroeder tone complexes consist of equal-amplitude tones with a starting phase (θ_n) which follows an algorithm developed by Schroeder (1970). The waveform of such tone complexes resembles a periodic series of linear downwards (Sch+) or upwards (Sch-) frequency sweeps, depending on the specific phase configuration. Sch+ and Sch-stimuli thus have identical power spectra, but differ in their phase spectra. Masked thresholds of tonal signals that are spectrally centered in the Schroeder tone complex have been found to be 5–25 dB lower in the Sch+ masker condition than in the Sch-masker condition (e.g., Smith et al., 1986;

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Kohlrausch and Sander, 1995), demonstrating that concepts based on the power of the stimuli, such as the power spectrum model of masking (e.g., Fletcher, 1940; Moore, 2003), fail to predict the perceptual results in these conditions. Instead, the threshold differences obtained with the Sch-vs. Sch+ maskers have been explored by analyzing the interaction between the stimulus phase spectrum and the phase transfer function of the auditory filter. If the phase curvature of an auditory filter, i.e. the second derivative of the corresponding phase transfer function, would be of the same size, but opposite in sign, as the phase curvature of the Sch+ masker, this should result in a highly modulated internal representation. In contrast, conceptually, the Sch-masker should lead to a flat, or less peaky, internal representation after the transformation through the same auditory filter. Thus, the peaky internal representation obtained in response to the Sch+ stimulus should be less effective as a masker than the Sch-stimulus, since the signal can be more easily detected in the dips of the peaky representation (e.g., Kohlrausch and Sander, 1995).

Following the hypothesis that minimum masking is achieved when the phase curvature of the stimulus is equal in magnitude but opposite in sign to that of the auditory-filter centered at the signal frequency, Oxenham and Dau (2001b) behaviorally estimated the auditory-filter phase curvature for a broad range of center frequencies (fc). However, it remained unclear to what extent effects of cochlear compression, level-dependent auditory filter bandwidth as well as properties of temporal envelope processing contribute to the observed masked patterns both in normal-hearing and hearing-impaired listeners (Oxenham and Dau, 2001a). Furthermore, such studies have assumed a roughly constant auditory-filter phase curvature within the auditory-filter's passband (e.g. Oxenham and Dau, 2001b; Kohlrausch and Sander, 1995; Lentz and Leek, 2001), which may only be a valid approximation in the frequency region around the center frequency but not throughout the entire passband of the filter (e.g., Shen and Lentz, 2009). Finally, in the psychophysical studies investigating auditory filter phase response (e.g., Lentz and Leek, 2001; Oxenham and Dau, 2001b; Shen and Lentz, 2009; Wojtczak and Oxenham, 2009) only the output from the auditory filter providing the highest signal-to-noise ratio (SNR) has typically been considered in the detection process (Moore, 2003). Thus, the correspondence of such behavioral estimates with the properties of the cochlear filters may be only qualitative and indirect.

Physiological responses would provide more detailed and local information about cochlear filter phase response. However, these are invasive and can only be obtained in animal studies. Indeed, physiological measures of BM responses to Schroeder tone complexes have been performed in chinchillas (Recio and Rhode, 2000) and guinea pigs (Summers et al., 2003). Both studies concluded that BM responses to Sch+ stimuli are "peakier" than the responses to Sch− stimuli, qualitatively consistent with the results from the psychophysical studies in humans described above. However, the connection between such physiological recordings in animals and the human cochlear phase response remains indirect.

In the present study, human auditory evoked potentials (AEP) were considered to investigate effects of local cochlear dispersion. In contrast to earlier studies that used broadband stimuli designed to compensate for "spatial dispersion" (i.e., travel-time differences across frequency) and, as a consequence, to create maximal neural synchronization *across* the cochlear partition (e.g. Dau et al., 2000; Junius and Dau, 2005; Elberling et al., 2007), the approach taken in the present study was *complementary* in the sense that *bandlimited* stimuli that were designed to compensate for "temporal dispersion" of the response at a restricted segment on the cochlear partition were used. It has been demonstrated that AEPs, such as auditory steady state responses (ASSR) obtained with narrowband stimuli (like amplitude modulated tones) can provide reliable and frequency-specific information, e.g. in connection to objective auditory threshold estimations (e.g. Picton, 2011). Here it was tested if properties of local cochlear dispersion can be represented by ASSRs obtained with an "optimized" (bandlimited) stimulation. Two stimulation paradigms were chosen: One of them considered Schroeder tone complexes as in the studies described above; the other one used narrowband stimuli, built from estimates of cochlear filter impulse responses (IR) as proposed by Irino and Patterson (2001). The IRs models have been argued to account for psychophysical masking data in humans (Rosen and Baker, 1994) as well as for auditory-nerve responses obtained from physiological measurements in cats (Carney et al., 1999). Here, the use of the temporally reversed IR as stimulus was hypothesized to theoretically produce a maximally peaky response at the output of the corresponding filter.

2. Method

2.1. Stimuli

Signal generation and data post-processing routines were implemented in Matlab, and the utility Playrec was used to manage the communication between Matlab and the soundcard. The digital-to-analog (D/A) conversion of the acoustic stimulus was performed at a sampling frequency, fs, of 48 kHz with a 24-bit resolution.

2.1.1. Schroeder tone complexes

Schroeder tone complexes were generated by adding harmonics between 0.4 and 1.6 times the center frequency (fc), following the study of Oxenham and Dau (Oxenham and Dau, 2001a). Sound pressure levels (SPL) of 45 and 70 dB were considered. f_c was set to 1 kHz and a fundamental frequency (f_0) of 90 Hz was chosen since a repetition rate of 90 Hz has been shown to produce strong ASSR primarily generated in the auditory brainstem (e.g., Picton, 2011). The initial phase of each harmonic was defined according to equation (1.1), where N stands for the total number of harmonics and C is a scalar, introduced by Lentz and Leek (Lentz and Leek, 2001) to allow sweep rate modifications.

$$\theta_n = C\pi n\frac{(n-1)}{N} \tag{1.1}$$

Three C values were tested for each level: $C = +1$ (corresponding to the original Sch+ stimulus), $C = 0$ and $C = -1$ (corresponding to the original Sch-stimulus). In the case of $C = 0$, all components were added with zero phase, resulting in a series of frequency-limited pulses. Schroeder tone complexes have a constant phase curvature, being positive for $C > 0$, zero for $C = 0$ and negative for $C < 0$. Thus, Sch+ complexes represent periodic sequences of linear downward frequency sweeps whereas Sch-tone complexes are temporally reversed, i.e. upward frequency sweeps. The phase curvature of a given Schroeder tone complex (Kohlrausch and Sander, 1995) amounts to:

$$\frac{d^2\theta}{df^2} = C\frac{2\pi}{Nf_0^2} \tag{1.2}$$

2.1.2. Gammachirp impulse responses

Gammachirp impulse responses (gc-IR) were also used as stimuli, generated using the model of Irino and Patterson (Irino and Patterson, 2001) and including level-dependent cochlear compression. The gc-IR represent upward frequency sweeps. As in the case of the Schroeder tone complexes, the corresponding temporally reversed stimulus was also considered, i.e. the reversed impulse response, gc-IR_{rev}, representing a downward frequency sweep. The IRs were obtained at fc = 2 kHz for 50 and 70 dB SPL and concatenated with a repetition rate of 80 Hz in order to obtain an integer number of samples per repetition.

2.2. ASSR recordings

2.2.1. Subjects

A total of 14 adult subjects participated in the experiments (9 males and 5 females), between 22 and 32 years of age (mean of 26 years). All subjects had normal hearing according to their pure-tone audiogram (≤20 dB HL). The study was approved by the Danish Science-Ethics Committee (Den Nationale Videnskabsetiske Komité) under the reference H-3-2013-004.

2.2.2. Apparatus

ASSRs were recorded in a double-walled, sound-attenuating and electromagnetic shielded booth. The Biosemi ActiveTwo System, an electroencephalography (EEG) recording system with active electrodes, was used for the recording of the ASSRs. The signal was played to the subjects in epochs of 1 s through an earphone (ER-2 insert earphone from Etymōtic Research Inc.).

The Biosemi ActiveTwo system was set at speed mode 6 with a decimation factor of 1/2, leading to a sampling frequency of 4096 Hz with 24-bit resolution. The hardware filter bandwidth follows a 5th order sinc response, with the −3 dB point located at 1/5th of the sampling frequency. The recording bandwidth limit with the described settings was 843 Hz, well above the 40–100 Hz modulation rates commonly used for ASSR recordings. The Biosemi ActiveTwo system uses two ground electrodes: Common Mode Sense (CMS, an active electrode) and Driven Right Leg (DRL, a passive electrode).

The electrodes were placed on the scalp by using an elastic cap with plastic electrode holders. The cap follows the standardized 10/20 electrode system with 64 electrode holders, but only signals from Cz (vertex electrode) and P10/P9 (behind the right/left ear), together with the CMS and DRL, were recorded. All ASSR results shown in the present study represent the Cz-P10 difference (right ear measurements) or the Cz-P9 difference (left ear measurement). The signals from the electrodes and the trigger were stored on a hard disk using the ActiView software.

2.2.3. Recording and analysis of ASSR

The recording sessions lasted about 2 h in the case of the Schroeder tone complexes and about 30 min in the case of the IR stimuli. The subjects were seated in a comfortable reclined chair and were encouraged to relax or sleep during the recordings.

The recorded EEG data were first filtered with a band-pass fifth order Butterworth filter (60–300 Hz) applied in both forward and backward directions. Epochs exceeding an amplitude threshold of ±80 μV were rejected. The non-rejected epochs were concatenated forming sweeps of 16 epochs, resulting in a spectral resolution of 0.0625 Hz/bin. The resulting sweeps were averaged, ideally reducing the noise term by a factor of the square root of the number of averaged trials.

An F-test statistical method was applied to the filtered and averaged EEG spectrum in order to objectively assess ASSR significance. The power at the ASSR frequency was compared to the power of the EEG background noise, defined as the power average at ±3 Hz (96 bins) from the ASSR frequency (F-ratio). At the ASSR bin, the power estimate represents a chi-squared variable with 2 degrees of freedom. In contrast, the power noise estimate is a chi-squared variable with 2·96 degrees of freedom (Dobie and Wilson, 1996). With the degrees of freedom of each variable and the F-ratio, the F cumulative distribution was calculated. The probability (p) of the ASSR power being at least as big as the current observation was calculated as a 1 − F cumulative distribution function, assuming that both noise and ASSR component came from the same distribution. If the null hypothesis ($p \leq 0.01$) was rejected, the ASSR component was considered statistically significant from the EEG background noise estimate (positive F-test).

A Kruskal-Wallis one-way analysis of variance was used to test whether the differences in ASSR magnitude for different conditions were statistically significant. A significance level of $\alpha = 0.01$ was chosen. If $p \leq 0.01$, the null hypothesis was rejected in favor of the alternative hypothesis, implying that the results came from different distributions.

2.3. Simulation of frequency selectivity and cochlear dispersion

BM motion simulations were obtained using a one-dimensional, linear transmission line model to illustrate effects of cochlear dispersion. The linear and passive version of the model developed by Epp et al. (2010) was chosen, which discretizes the cochlea into 1000 equally spaced segments. The ratio between the resonance frequency of each segment and the half-power bandwidth, the quality (Q) factor, was set to be constant along the segments. Different Q-factors were used to simulate different stimulus levels to reflect level dependent BM tuning (Epp et al., 2010).

3. Results

3.1. ASSR recordings

Fig. 1 shows the ASSR magnitudes in response to the Schroeder tone complexes as a function of the C value. The results for the individual subjects are shown in the upper panels for the stimulation levels of 45 dB SPL (left) and 70 dB SPL (right). The gray scale of the symbols indicates the SNR of the response on a dB scale. The single open symbol indicates that the response in this particular condition (C = 1) was not significant for one of the subjects (RSL). The lower panels show the corresponding median values across subjects as well as the 25th (q1) and 75th (q3) percentiles, relative to the results obtained in the C = 0 condition. The data from the subject RSL was excluded in the lower left panel due to the non-significant response for condition C = 1. Overall, the ASSR amplitude elicited with the Schroeder tone complexes was found to be significantly larger for C = −1 than for C = +1, both at 45 dB SPL ($\chi^2(1) = 12.79$, $p < 0.001$) and at 70 dB SPL ($\chi^2(1) = 14.29$, $p < 0.001$). No differences were observed across levels for C = −1 ($\chi^2(1) = 1.93$, $p = 0.165$) and C = +1 ($\chi^2(1) = 3.23$, $p = 0.072$).

Fig. 2 shows the ASSR magnitude in response to the gc-IR and its temporally reversed version, gc-IR_{rev}. The upper panels represent the data obtained for the individual subjects at 50 dB SPL (left) and 70 dB SPL (right). As in Fig. 1, the SNR of the different recordings is represented using a gray scale, in dB, and the single open symbol indicates that the corresponding response was not significant in the condition gc-IR for subject MN. The lower panels in Fig. 2 show the ASSR magnitude relative to the mean of the two responses. At both stimulus levels, the response amplitude

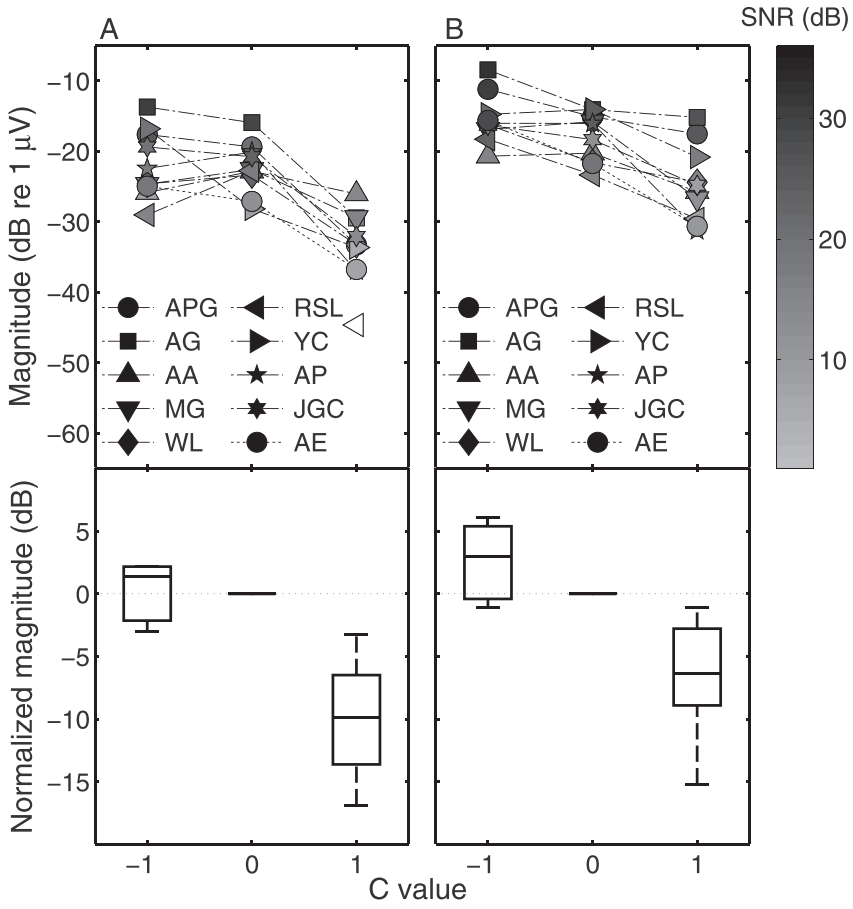

Fig. 1. Measured ASSR magnitudes in response to the three Schroeder tone complexes (with C = −1, C = 0, C = 1) for the stimulation levels of 45 dB SPL (left) and 70 dB SPL (right). The data for the individual subjects are shown in the upper panels. The grey scale represents the SNR of the recordings, in dB. The lower panels show the normalized magnitude with respect to the response at C = 0 for each subject.

obtained with gc-IR and gc-IR$_{rev}$ did not differ significantly from each other ($\chi^2(1) = 2.96$, $p = 0.085$ for 50 dB SPL; $\chi^2(1) = 0.46$, $p = 0.496$ for 70 dB SPL).

3.2. Simulation of frequency selectivity and cochlear dispersion

Fig. 3 shows the simulated BM responses to the Schroeder tone complexes. The solid black waveform represents the response of the filter tuned to the center frequency of the tone complex (1 kHz), referred to as the "on-frequency" response. The responses at the four other frequencies are shown as gray functions and represent "off-frequency" responses. The upper panel in Fig. 3 shows the simulations for the C = −1 condition. The middle and low panels show the corresponding results for C = 0 and C = 1, respectively. Above each of the three panels, the corresponding stimulus waveforms are shown for comparison.

The filtered stimuli in the case of C = −1 (upper panel) exhibit relatively flat envelopes in the individual frequency channels. For C = 0 (middle panel), the "response" envelopes are more peaky in the different filters and the response maxima are shifted in time across frequency. The temporally most compact response at the center frequency (1 kHz) can be seen for C = +1 (bottom panel). However, this effect is less pronounced, or absent, in the off-frequency channels. In particular, for this condition, there is a large phase shift of the individual channel responses across frequency.

Fig. 4 shows the simulated responses to gc-IR (left panel) and its temporally reversed version (gc-IR$_{rev}$; right panel). The stimulus waveforms are indicated above the filtered model outputs. The differences between the responses to gc-IR and gc-IR$_{rev}$ are more subtle than in the case of the Schroeder-tone complexes since the stimulus bandwidth is much smaller than for the impulse response stimuli. Nevertheless, the same principal pattern can be observed in the results: First, the simulated response at the stimulus center frequency (2 kHz) is temporally more compact for gc-IR$_{rev}$ than for gc-IR. Second, the response peaks in the off-frequency channels provide stronger phase shifts across frequency in the case of the gc-IR$_{rev}$ stimulation than in the case of the gc-IR stimulation.

4. Discussion

ASSR with narrowband stimuli, like amplitude modulated tones, have been demonstrated to represent an objective estimate of frequency-specific sensitivity (e.g., Purcell et al., 2004; Herdman and Stapells, 2001). The present study tested, inspired by psychoacoustic masking data and auditory modeling studies, if ASSR to specific stimuli would be suitable for estimating effects of local (frequency-specific) cochlear dispersion in humans.

The hypothesis was that the Schroeder tone complex with positive phase curvature (C = 1) would compensate for phase delays *within* the transfer range of the BM filters at and around

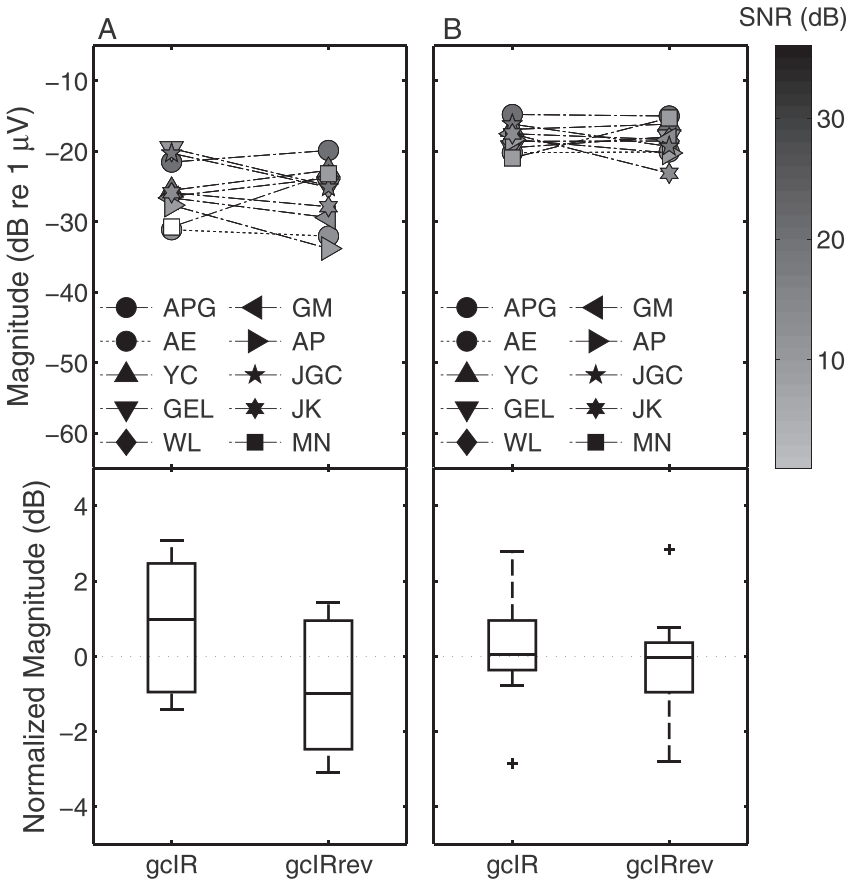

Fig. 2. ASSR magnitude in response to the gc-IR at 2 kHz for stimulus levels of 50 dB SPL (panel A) and 70 dB SPL (panel B). The data from the individual subjects are shown in the upper panels. The gray scale represents the SNR of the recordings, in dB. The lower panels show the normalized response magnitude relative to the mean of the response for each subject.

the chosen stimulus center frequency (of, in this case, 1 kHz). It was anticipated that such processing would lead to a peaky internal representation after cochlear filtering at the center frequency, consistent with corresponding physiological near-field recordings in the cochlear nucleus of the chinchilla (Recio, 2001) and in line with the simulations of the filtered stimuli at the output of the BM (Fig. 3). The obtained ASSR data from the present study (Fig. 1) demonstrated, however, that the Sch+ stimulus (C = 1) actually produced the *smallest* response amplitude whereas the temporally reversed stimulus (Sch−, C = −1) produced the largest response amplitude. Moreover, no differences were observed between the (normalized) ASSR magnitudes obtained with the Sch+ stimulus (C = 1) at the two different sound pressure levels (left versus right panel in Fig. 1). In contrast, the psychophysical data from Oxenham and Dau (2001b) demonstrated a large effect of level for corresponding Sch+ stimuli suggesting a level dependent (auditory filter) phase function. If the ASSR would be sensitive enough to reflect (on-frequency) dispersive effects, a smaller ASSR magnitude should be expected for the lower level than for the higher level, consistent with the hypothesis of a fast-acting compression mechanism that is more effective at the lower level (Carlyon and Datta, 1997). The results demonstrate that the chosen method and/or stimulation paradigm are not appropriate, or not sensitive enough, to represent frequency-specific cochlear phase effects.

The simple simulations with the linear BM model (Figs. 3 and 4) suggested that, even though dispersive effects in the on-frequency channel may be represented at a peripheral level, the across-frequency asynchrony of the BM excitation may dominate the “summed” response. It is important to note that a proper simulation of the ASSR would require a more realistic model of auditory peripheral and retro-cochlear processes as well as a transformation of the neural firing rates at the neural generator sites via convolution with the “unitary response” to the measured response at the electrodes in the far field (e.g. Melcher and Kiang, 1996; Dau, 2003; Rønne et al., 2012; Verhulst et al., 2015). Such more detailed modeling was not attempted here since the main motivation of the present study was to evaluate experimentally if the evoked potentials to the sequences of (bandlimited) chirps can represent properties of local cochlear dispersion.

Auditory evoked far-field responses represent synchronization potentials that are more pronounced the larger the number of simultaneously activated neurons. This is particularly evident for responses that are mainly generated at peripheral and brainstem levels, such as compound action potentials (CAPs), auditory brainstem responses (ABR) and auditory steady-state responses (ASSR). The role of synchrony of neural activity across the whole cochlear partition has been demonstrated in ABR and ASSR studies by using *broadband* rising chirps instead of clicks of similar bandwidth. If the stimulus compensates for the travel-time differences across frequency, as in the case of the rising chirp, the corresponding evoked potential exhibits a larger amplitude than in the case of the click and falling chirp stimulation (Dau et al.,

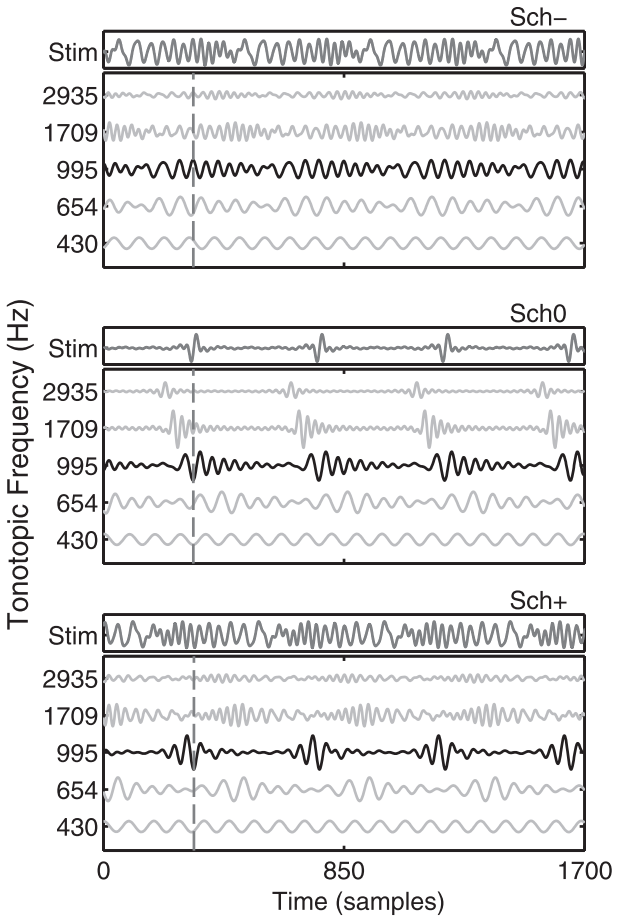

Fig. 3. Simulations obtained with the BM transmission-line model of Epp et al. (2010) in response to the Schroeder tone complexes. The stimulus waveforms for C = −1 (top), C = 0 (middle) and C = +1 (bottom) are shown above the respective filtered model outputs. The on-frequency responses (at 1 kHz) are represented in black while four off frequency responses are shown in gray. The vertical dashed line indicates the temporal position of one of the peaks of the on-frequency response.

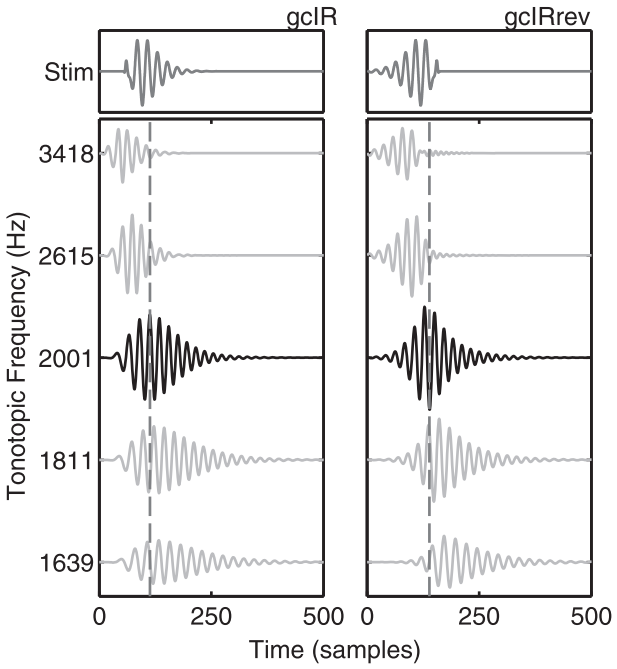

Fig. 4. Simulations obtained with the BM transmission-line model of Epp et al. (2010). On top of the figure, the input stimuli are shown: gc-IR (left) and gc-IRrev (right). The on-frequency responses (at 2 kHz) are represented in black while four off-frequency responses are shown in gray. The vertical dashed line indicates the temporal position of the maximum of the on-frequency response.

2000; Elberling and Don, 2008), despite the fact that the individual within-channel contributions are less compact in time in the case of the rising chirp compared to those of the other stimuli (e.g., Uppenkamp et al., 2001; Buss et al., 2002). In the case of the stimuli chosen in the present study to compensate for local dispersion, still the ASSR response is dominated by the synchronized activity across frequency which is more effective for the stimulus that exhibits smaller phase delays in the filtered representations across frequency (the Sch-stimulus) than for the Sch+ stimulus. This is the case for the 1800-Hz wide Schroeder tone complexes and is also still represented in the simulations with the narrowband IR stimuli (Fig. 4) even though the corresponding ASSRs (Fig. 2) with these stimuli did not show any significant differences.

It is possible that other stimulation paradigms, potentially with additional noise masking to suppress "off-frequency" contributions, are more effective than the ones considered here. Furthermore, higher-level, cortical, responses to tonal target tones in the presence of the different types of Schroeder tone complexes (as maskers) have been demonstrated in a magneto-encephalography (MEG) study to be correlated with the corresponding behavioral masked thresholds of the tones (Rupp et al., 2002). The investigation provided in the present study demonstrates that the brainstem responses, as reflected in the ASSR, do not reflect frequency-specific cochlear dispersion despite the fact that ASSR are commonly used to estimate frequency specific hearing sensitivity.

5. Conclusion

ASSRs to Schroeder tone complexes that had earlier been used in behavioral masking studies to estimate auditory filter phase response were found in the present study to be dominated by "across-channel" synchrony and, thus, do not reflect local place-specific information. In the case of the more frequency-specific impulse response stimuli, no significant differences were found between the responses to the rising versus falling frequency sweeps. Thus, whereas ASSRs to narrowband stimuli have been considered as an objective indicator of frequency-specific hearing sensitivity, the paradigms tested in the present study do not seem to be sensitive enough to reflect local cochlear dispersion.

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